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Original Article

Conceptualizing the Autism Spectrum in Terms of Natural Selection and Behavioral Ecology: The Solitary Forager Hypothesis

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Abstract: This article reviews etiological and comparative evidence supporting the hypothesis that some genes associated with the autism spectrum were naturally selected and represent the adaptive benefits of being cognitively suited for solitary foraging. People on the autism spectrum are conceptualized here as ecologically competent individuals that could have been adept at learning and implementing hunting and gathering skills in the ancestral environment. Upon independence from their mothers, individuals on the autism spectrum may have been psychologically predisposed toward a different life-history strategy, common among mammals and even some primates, to hunt and gather primarily on their own. Many of the behavioral and cognitive tendencies that autistic individuals exhibit are viewed here as adaptations that would have complemented a solitary lifestyle. For example, the obsessive, repetitive and systemizing tendencies in autism, which can be mistakenly applied toward activities such as block stacking today, may have been focused by hunger and thirst toward successful food procurement in the ancestral past. Both solitary mammals and autistic individuals are low on measures of gregariousness, socialization, direct gazing, eye contact, facial expression, facial recognition, emotional engagement, affiliative need and other social behaviors. The evolution of the neurological tendencies in solitary species that predispose them toward being introverted and reclusive may hold important clues for the evolution of the autism spectrum and the natural selection of autism genes. Solitary animals are thought to eschew unnecessary social contact as part of a foraging strategy often due to scarcity and wide dispersal of food in their native environments. It is thought that the human ancestral environment was often nutritionally sparse as well, and this may have driven human parties to periodically disband. Inconsistencies in group size must have led to inconsistencies in the manner in which natural selection fashioned the social minds of humans, which in turn may well be responsible for the large variation in social abilities seen in human populations. This article emphasizes that individuals on the autism spectrum may have only been partially solitary, that natural selection may have only favored subclinical autistic traits and that the most severe cases of autism may be due to assortative mating.

Keywords: autism, comparative neuroscience, ecology, epidemiology, neuroethology, systemizing

Autism and Natural Selection

Autism is a condition that affects individuals from birth or infancy and is diagnosed on the basis of three primary symptoms: social deficits, impaired communication and stereotyped and repetitive behaviors (Piven, 2000). People with autism largely withdraw from social contact and become absorbed in private worlds of obsessive interests and repetitious activities (Kelly, Garnett, Attwood, and Peterson, 2008). Autism has been shown to be highly heritable and has been associated with a number of both genetic and environmental risk factors (Cantor, 2009). It is thought that the genes associated with autism create very selective abnormalities that tend to affect brain regions associated with social cognition (Amaral, Schumann, and Nordahl, 2008). Unfortunately, the genetics, molecular biology and neuroscience of autism are still, relative to many other neurological disorders, shrouded with uncertainty due to their highly complex nature (O'Roak and State, 2008).

A portion of this complexity and uncertainty arises from the relatively large number of distinct susceptibility genes that have been identified, many of which can be completely absent even in pronounced autism (Freitag, 2007). This genetic heterogeneity may be responsible for the clinical heterogeneity, which ranges from debilitating social deficits to minor personality traits (Caronna, Milunsky, and Tager-Flusberg, 2008). Medical science recognizes certain phenotypes that are thought to lie on a continuum often referred to as the autism spectrum disorders (ASD). Of these disorders, the DSM recognizes: autistic disorder (Kanner's autism), childhood disintegrative disorder, and pervasive developmental disorder not otherwise specified (PDD-NOS, or atypical autism) (Piven, 2000). Autistic disorder itself has also been broken into 4 subgroups: Asperger syndrome the highest-functioning form (Asperger, 1944; Frith, 1991), autism, high-functioning and low-functioning autism (Kanner, 1943; Baron-Cohen, 2006). Geneticists report that although the clinical distinctions do not map neatly onto specific genes or patterns of genes, lower functioning individuals may have a higher total number of susceptibility alleles (Abrahams and Geschwind, 2008). For this reason this article will not make evolutionary distinctions between individual autistic disorders but will focus on the autism spectrum and the range of related genes as a whole.

A number of very different theories about the causes of autism have attempted to explain the scattered facts. It has been difficult for theorists to create a grand synthesis, and autism has been reconceptualized many times. At one point, it was thought that autistic children were purely a result of poor parenting, an idea that was once widely embraced but is now utterly rejected (Baron-Cohen and Bolton, 1993). Autism is now known to be a biological phenomenon in which a genetic diathesis or susceptibility may interact with early environmental circumstances to determine the severity of outcome (Kumar and Christian, 2009). However, why this genetic susceptibility to autism is so prevalent and how the genes persisted despite the perceived negative effects is unclear. It is the author's

view that conceptualizing autism in terms of evolutionary biology will offer insight into the underlying factors, and help to make sense out of its seemingly incongruous characteristics.

The risk of developing autism approaches .5 percent in the general population, making it a highly prevalent "disorder" from an evolutionary perspective (Gluckman, Beedle, and Hanson, 2009). In the past two decades alone, the incidence of ASD has increased from 2-5 to 15-70 per 10,000 children, a dramatic increase, which is attributed to heightened attention by the medical community as well as the broadening of diagnostic criteria (King and Bearman, 2009; Fombonne, 2009). Disorders, like autism, that are so prevalent that they exceed common mutation rates are thought to have persisted because the genes responsible for them conferred some advantage in the ancestral environment (Nesse and Williams, 1998). To fully understand the evolutionary provenance of such a syndrome it is important to attain a rough date of its origins in natural history.

For years autism was thought to be a disorder that affected Caucasians exclusively. If this had in fact been the case, an evolutionary explanation would have to explain why autism originated and spread in Europe over the last 20 to 40 thousand years. It is now known, however, that autism affects all human populations (Szatmari and Goldberg, 2000). In fact, autism presents with very similar prevalence rates, worldwide, in all studied races and ethnic groups (Fombonne, 2002) and has only a very moderate association with immigrant status or socioeconomic status (Morrier, Hess, and Heflin, 2008). That autism has similar prevalence in all studied ethnic groups strongly suggests that it existed in a fully developed form well before the first humans left Africa. Autism and the autism spectrum appear to be very ancient, yet how were the responsible genes selected and maintained over tens or perhaps hundreds of millennia?

This article will delineate the "solitary forager" hypothesis of autism which proposes that some genes contributing to autism were selected and maintained because they facilitated solitary subsistence. Population dispersion, band fission or dissolution, estrangement, ostracism, and separation were probably infrequent but unavoidably reoccurring conditions that may have impacted the human genome during evolution. Individuals on the autism spectrum are described here as having had the potential to be self-sufficient and capable foragers in scenarios marked by diminished social contact. In other words, these individuals, unlike neurotypical humans, would not have been obligately social and may have been predisposed toward taking up a relatively solitary lifestyle. Common psychological characteristics of autism are taken here as a suite of cognitive adaptations that would have facilitated lone foraging. Like other solitary mammals with similar cognitive adaptations, they were probably not completely solitary; rather, they may have done much of their foraging alone and reconvened intermittently with familiar individuals. The article will use the perspectives from evolutionary medicine and evolutionary psychopathology to expound upon this hypothesis in a conjectural and exploratory manner. Corroborating evidence is sought from evolutionary medicine, the systemizing theory of autism, anthropology, primatology and comparative neuroscience.

Autism and Evolutionary Medicine

Many medical conditions that are pathological in the present are known to have been adaptive in the ancestral environment, and the science of evolutionary medicine is concerned with identifying and understanding these conditions (Williams and Nesse, 1991). It is thought that evolutionary perspectives on disease can elucidate pathophysiology and ultimately inform treatment strategy (Gluckman et al., 2009). The accomplishments of evolutionary medicine in explaining disease in terms of adaptation to environment are extensive and have provided insights into the origins of atherosclerosis, cardiovascular disease, cystic fibrosis, diabetes mellitus, obesity, sickle cell anemia and many others (Trevathan, 2007). Evolutionary medicine has also attempted to explain the origins of certain mental disorders. Several well-received theories have been formulated based on these attempts and they may lend perspective to the natural history of autism.

The growing fields of evolutionary psychopathology (Nesse, 1999; Baron-Cohen, 1997), and evolutionary psychiatry (Brune, 2008; Panksepp, 2006) are concerned with the application of evolutionary rationale to the understanding of psychological and psychiatric disorders. Researchers in these domains have concluded that there were multiple, alternative cognitive strategies used to deal with the problems and obstacles that recurred in our evolutionary past (Cosmides and Tooby, 1992). Furthermore, they have emphasized that individual differences in developmental patterns may not always represent the effects of idiosyncratic life experiences, but in fact represent biological, naturally selected responses to pressing environmental concerns (Bjorklund and Pellegrini, 2000; Hood and Jenkins, 2008).

A number of sensible evolutionary theories of autism have been put forth. Autism has been conceptualized as a low-fitness extreme of a parentally-selected fitness indicator (Shaner, Miller, and Mintz, 2008). The authors have advanced that variation in the ability to connect socially to ones parents, an adaptive trait, may have a maladaptive, extreme form that results in autism. Other researchers have envisioned autism as a consequence of paternally imprinted genes (Badcock and Crespi, 2006). This idea has been taken further and autistic-like traits have been envisioned as constituting a male-typical strategy geared toward parental investment, low-mating effort, high partner-specific investment and long-term resource allocation (Del Giudice, Angeleri, Brizio, and Elena, 2010). These and other theories of autism are well-supported and plausible. None of these are directly compatible with the present hypothesis but neither are they directly contradictory. Like the present hypothesis they view autism as an extreme end of a continuum constituted by adaptive traits. Unlike these though, the present hypothesis attempts to explain autism in terms of the behavioral ecology of hunting and gathering.

Many articles in the last two decades have attempted to utilize the perspective of behavioral ecology to explain various forms of psychopathology (e.g., anxiety, addictive personality, depression, obsessive compulsive disorder, psychopathy and post-traumatic stress disorder (PTSD)). These articles have attempted to reconceptualize these disorders as adaptive, cognitive syndromes that, at one time, had ecological utility (Hood and Jenkins, 2008; Reser, 2006). These articles have given thoughtful treatments to disorders such as: anxiety, hypothesized to represent a careful, cautious strategy (Marks and Nesse, 1994); depression, a socially submissive strategy (Allen and Badcock, 2006); schizophrenia, a defensive, vigilant and impulsive strategy (Reser, 2007); psychopathy, a socially selfish

and opportunistic strategy (Brune and Brune-Cohrs, 2006); and PTSD, a threat-avoidant strategy (Bracha and Maser, 2008). Significant comparative evidence supports these four theories. The symptoms of anxiety, depression, psychopathy and PTSD have been shown to exist in other animals, serving adaptive purposes. Imagine the plight of a guppy born without the capacity for predator anxiety or a social monkey born without the instinct to act subordinate to larger, dominant monkeys. Despite the cultural stigma and psychological pain associated with these four disorders today, genetic susceptibility to them would have conferred specific adaptive benefits in prehistoric times. Certainly, a person who meets the criteria for an anxiety disorder takes this "cautious strategy" to an extreme; however, researchers speculate that such people may have achieved high reproductive success during highly volatile, violent or unpredictable times (Nesse, 2007). Similarly, self-subordination, threat-avoidance and selfishness all represent important behavioral proclivities that have strong neurological foundations in a large variety of species. Importantly, social and asocial tendencies also have neurological bases and vary widely between species (Robinson, Fernald and Clayton, 2008). Innate predispositions toward sociality are also thought to vary within species (Brune and Brune-Cohrs, 2006), and it is thought that the severity of autism, like the severity of these other disorders, can be shown to exist on a continuum. As a final example of the success and applicability of evolutionary psychopathology to mental disorder, let us consider the popular reconceptualization of attention-deficit / hyperactivity disorder (ADHD).

Thom Hartmann (1997) coined the phrase "hunter in a farmer's world" to explain the predicament of individuals with ADHD. He totally rethought the condition, explaining that in the ancestral environment, children were not naturally selected to listen for hours on end, to pay careful attention to lessons, or to concentrate for long periods on assignments. Shapiro and others (Jensen et al., 1997) have elaborated on this hypothesis. They explained that the predilection for individuals with ADHD to be impulsive, hyperactive and scattered could have offered advantages in prehistoric times. It is likely that the ability to focus on a single concept for a prolonged period was not necessarily beneficial in hunting and gathering times. High levels of activity and scanning, though, may have kept humans in tune with a rapidly changing environment and allowed them to identify and act on both immediate threats and immediate opportunities. Additionally, Panksepp (1998) has concluded that even some severe cases of ADHD may reflect normal variation in these adaptive tendencies. Likewise, this article will take the perspective of evolutionary psychopathology and make the argument that autism represents "a lone forager in a social world." As with ADHD, perhaps a large proportion of the autism spectrum, maybe even pronounced cases of autism, may reflect normal variation. The autism spectrum will be conceptualized as representing naturally occurring variation, at one extreme end of the sociality continuum.

Presentation of the Hypothesis

Today, the cognitive disabilities associated with the autism spectrum are clear and well documented; however, modern social, occupational, and mating practices may conceal the evolutionary or adaptive benefits. From an anthropological perspective, the society we

live in is very different from the ancestral environment. Because of the large group sizes seen in modern day cities and the very social nature of modern employment, social abilities such as congeniality, extraversion and savoir-faire are highly regarded. Even minimal social dysfunction or awkwardness can be professionally and socially problematic. In fact, the DSM considers social ability as a critical component of psychological health (APA, 1994). Social ability may have been less critical though in the prehistoric past, especially within certain contexts. During the six million years since our branch diverged from that of chimpanzees, our ancestors lived in relatively small groups that probably fluctuated greatly in size (Nesse and Williams, 1995). Under these conditions, the abilities to relate effortlessly to a stranger, to display affection in a demonstrative manner, or to charm a foraging companion were probably exposed to inconsistent selective pressures. Inconsistencies in the level of social ability that our environment demanded may well be responsible for the large variation in social abilities seen in human populations, as well as the extremes of social "dysfunction."

The adaptive value of social ability may have been inconsistent in the ancestral past for many reasons. Depending on the period of human evolution, the geographical location, the ecological setting and the cultural habits of the group in question, ancestral foragers may have foraged intimately with others throughout the day, may have spent weeks foraging alone, or anything between these two extremes. Humans are a highly social species, and this tells us that, like chimpanzees, we must have spent much of our formative years congregating together (Byrne and Bates, 2007). However, just as our social tendencies are a testament to our social past, our asocial tendencies may indicate the opposite. In other words, during prehistoric times, a certain proportion of breeding individuals may have adapted neurologically to living under conditions where group size was very small or social contact was attenuated, and this may have led to the numerous autism genes found in the modern-day gene pool. It is unclear which phenotypes on the autism spectrum might have been selected for in the ancestral environment. Surely it is most conservative and parsimonious though to assume that high-functioning or subclinical phenotypes were the substrate for selection.

Certain eccentricities or impediments peculiar to autism may have precluded past researchers from considering that individuals on the autism spectrum may have survived well during prehistoric times. As in neurotypical individuals, behavior in autism can vary markedly from individual to individual. Some individuals with autism are awkward and unwieldy while others are graceful and nimble. Some are gentle and kind while others can become angry and violent. Some are severely mentally handicapped whereas others are cognitively gifted. These extremes, often barely tempered by social constraints and morays, might make these individuals appear dangerously unnatural. Given this, and given that a proportion of individuals with autism cannot be mainstreamed comfortably in elementary school, it may appear that autism would have been maladaptive. Hypothetically though, it would be much more difficult to place a young orangutan in a human elementary school classroom than it would be to place the average autistic child, and yet orangutans are capable of reaching full ecological independence before age 10 (Wich, Atmoko, and Setia, 2009). Although, some individuals on the autism spectrum have grave social deficits, many may have been able to survive and prosper as effectively as other solitary mammals in their

natural environment. A great deal of new research supports this line of reasoning by illustrating that autistic individuals may have great trouble with social cognition but that their other cognitive abilities are largely intact (Baron-Cohen, 2003). The next section will consider some of the findings in the literature on autistic intelligence, supporting the notion that autistic individuals can be very competent in areas that do not require social cognition.

Testing the Hypothesis

Autistic intelligence and systemizing

Simon Baron-Cohen and others have changed the way that many researchers think about autism by pointing out that a social deficit alone may account for most of the symptoms. Previous theories of autism have characterized autistics as cognitively confused, disorganized or incoherent. Baron-Cohen, on the other hand, has characterized autistics as having profound social disabilities but otherwise being coherent and able-minded. His theories of autism emphasize that the main deficit is in the social domain, specifically, in the inability to empathize with and model the minds of others (Baron-Cohen, 1995). A large number of subsequent studies have substantiated that "theory of mind," or the ability to empathize with others, is impaired in autism (Colle, Baron-Cohen, and Hill, 2007). Baron-Cohen and others have argued persuasively that impaired theory of mind in autism can be independent of learning ability and general intelligence. Furthermore, he has documented that some autistic individuals can have superior technical understanding of physical systems (sometimes referred to as folk physics as opposed to folk psychology) compared to their age-matched peers, and he has termed this ability "systemizing."

Baron-Cohen has demonstrated that even though autistics are poor at empathizing, they are good at systemizing. Systemizing is the ability to observe a physical system and make inferences or conclusions about how it works and what causes it to work the way it does. He explains that systemizing works well for phenomena that are lawful and deterministic but that systemizing is of almost no use when it comes to predicting moment-by-moment changes in a person's behavior. Empathizing and forming theories about the other person's mind is required for the latter task (Baron-Cohen, Ashwin, Ashwin, Tavassoli, and Chakrabarti, 2009). According to Baron-Cohen, abilities that are associated with empathizing include responding empathetically to distress, intuiting another's emotional state, being sensitive to facial expressions, and demonstrating ability with language. Systemizing, on the other hand, is associated with ability in domains such as map reading, mental rotation, physics, mathematics and motoric systems (Baron-Cohen, 1995). People who are good at empathizing are thought to lean toward jobs in the areas of social work, psychology, and nursing. High systemizing is thought to lead to jobs in engineering, construction, and science. Baron-Cohen has even indicated that he thinks that autistic traits may have been naturally selected due to their contribution to tool construction and use (Baron-Cohen, 2003).

Unlike autism, empathizing seems to be unimpaired in individuals with Down syndrome, William's syndrome, and some other forms of mental retardation, despite their decreased ability to systemize and their lower general intelligence (Baron-Cohen, Leslie, and Frith, 1986; Karmiloff-Smith, Grant, Bellugi, and Baron-Cohen, 1995). This

dissociation between intelligence and empathy indicates a real genetic and cognitive difference between the two types of disorders. Many children with autism have IQs well below the average for their age; however, the intelligence tests that correct for social disability have shown that many autistics may in fact not be intellectually impaired at all (Scheuffgen, Happe, Anderson, and Frith, 2000). Contrary to speculations, researchers have found little evidence of a deficit of executive function in autistic children younger than 4 years of age. This suggests that the mild executive function deficits seen after age 4 are not primary to the disorder but may arise later because of the absence of social learning (Griffith, Pennington, Wehner, and Rogers, 1999). In fact, several "less learned, more innate" executive functions, including inhibition and visual working memory, appear to be spared in autism (Russell, 1997).

Baron-Cohen, and those who have followed him, has performed a great deal of research showing that systemizing is part of the genetic profile of autism and that the autistic spectrum is continuous with normal human variation. He has demonstrated that the parents and relatives of people with autism are good at systemizing but not very good at empathizing. He has compiled data showing that fathers and grandfathers of males with autism are twice as likely to be engineers compared to males in the general population (Baron-Cohen, 2006). He has also shown that students in the natural sciences have a higher number of relatives with autism than do students in the humanities (Baron-Cohen, 2006). Baron-Cohen and others have also shown that in Asperger's syndrome and in high-functioning autism, individuals can perform at normal or often superior levels in tasks requiring the systemization of information. People with Asperger's scored higher on his Systemizing Quotient (SQ) (Baron-Cohen, Richler, Bisarya, Gurunathan, and Wheelwright, 2003), performed better on tests of intuitive physics (Lawson, Baron-Cohen, and Wheelwright, 2004) and can reach extremely high levels of achievement in systemizing domains, such as mathematics, physics, and computer science (Baron-Cohen, Wheelwright, Stone, and Rutherford, 1999). This has been called the "autism advantage" in popular autism advocacy. It is thought that these high-functioning autistic individuals may be neurologically well-suited for certain jobs that are detail-oriented, repetitive, and involve the identification of technical errors (Scheuffgen et al., 2000). A popular conceptualization of this purports the idea that quirky computer specialists working in Silicon Valley, for example, desire jobs allowing them to work alone on computing problems, tend to marry others who are high on systemizing but low on empathy, and tend to have a propensity to have children that, like them, are on the autism spectrum. Baron-Cohen pointed out that, "If systemizing talent is genetic, such genes appear to co-segregate with genes for autism (Baron-Cohen, 2006, p. 868)."

Baron-Cohen has extended his theories into the "extreme male brain theory" of autism (Baron-Cohen, 2003). He pointed out that women, when compared to men, are more verbal, more socially adept, and have more sophisticated capacities for empathy and theory of mind. He asserted that the differences between non-autistics and autistics could be thought of as analogous to the differences between women and men. This extreme male brain theory is fascinating, well-supported, and may produce testable hypotheses. Baron-Cohen's analogies may be expanded if one concludes that autism represents the cognitive style of an individual who is well-suited for living alone. Comparing non-autistic and

autistic individuals then may be more like comparing a dog (a pack animal) to a cat (a largely solitary animal) rather than comparing a woman to a man.

Baron-Cohen and others have been successful in convincing many researchers that autistic people are intelligent in a different way and very good at systemizing and understanding non-social, natural processes. Baron-Cohen has even posited that evolution may have maintained the genes for autism precisely because of the systemizing ability, suggesting also that many cases of autism may be due to the assortative mating of two high-systemizing parents (Baron-Cohen, 2006). The present paper hopes to extend these arguments by pointing out that these natural systemizing abilities could have predisposed people on the autism spectrum to be able-minded, able-bodied, solitary foragers in the prehistoric past.

Autistic intelligence and foraging

In modern society, due to cultural, historic, and sociological circumstances, many individuals with autism do not learn to become self-sufficient. Due to their social deficits, many people with autism do not follow their peers on a path toward social and occupational mobility. Today, children must go through a prolonged period of education and socialization to reach a point where they can hold a job and live autonomously. Autonomy and even food procurement depend on social abilities as well as learning that took place in a particularly social setting, the school classroom. Schooling can be very difficult for individuals with autism because, as the systemizing theory of autism has demonstrated, individuals with autism have a proclivity to learn things on their own rather than from others (Siegel, 2003). Unfortunately, the interests chosen and knowledge acquired by individuals with autism often do not coincide with financial, professional, or social opportunities (Cimera and Cowan, 2009). Even when carefully guided by loving parents, it is difficult for many individuals with autism to teach themselves how to become self-sufficient in today's world. However, this may have been much more natural in the ancestral environment, particularly considering that merely 10,000 years ago, neither food procurement nor the acquisition of a place to sleep were necessarily contingent on social ability as they are today. The discipline of behavioral ecology, which may be applicable here, is based on the premise that behavioral traits, and the neural substrates responsible for them, are shaped by natural selection and hence are fine-tuned to respond to a particular environment (Krebs and Davies, 1993). The autism spectrum may be explicable in terms of behavioral ecology in the sense that it represents the adaptive value of being fine-tuned to thrive in an environment with diminished social contact.

Similar to mothers in contemporary foraging societies, mothers in the ancestral past would have required their children to learn how to forage for food from an early age (Buss, 2005). Virtually all mammals, whether of social or asocial species, use their systemizing abilities to learn food procurement techniques from their mothers (Krebs and Davies, 1993). The offspring of asocial mammalian species may not be motivated to empathize or socialize much with their mother, but are nonetheless driven by hunger to attend to her examples and internalize her tactics (Begon, Townsend, and Harper, 1996). This strategy works well for hundreds of species of asocial mammals (even ones with very small brains and limited systemizing abilities) and presumably would have worked well for individuals

with autism. Of course, it would be an immoral experiment to place an autistic toddler and its mother in the wilderness for years in order to see if he or she learns and thrives. However, would such an experiment be needed if it could be shown that autistic behaviors are normal relative to those of other solitary animals taken out of the wild since birth (e.g., a pet reptile, a domestic cat, or a captive orangutan)? Are there reasons to think that an individual with autism, living in prehistoric times, would not be strongly motivated by thirst, appetite, discomfort, sexual urges, and other innate instincts to become nutritionally independent and to increase its reproductive success?

The behavior of autistic individuals is often seen as bewilderingly inappropriate in a social context, because they so often become interested in or obsessed with socially meaningless activities (Piven, 2000). In a natural environment though, it is likely that hunger would have motivated them to redirect their obsessive tendencies toward food procurement. Today, their hunger for food does not drive them to refine food procurement techniques because their parents feed them every time they are hungry. Modern humans are responsible for social and academic learning and are rarely given the chance to be positively reinforced by successful food acquisition. This temporal or causal pairing between learning and satiety, integral for wild animals (Domjan, 2003), has been artificially taken away from modern children. Because the compelling and coercing natural instinct of hunger does not actuate or motivate modern individuals with autism, their efforts and skills are misplaced onto irrelevant stimuli.

The powerful and mobilizing asocial fascinations and preoccupations seen in modern-day autism could have aided their prehistoric counterparts in self-preservation. Humans habituate to things that they are not interested in and systemize things that they find rewarding, motivating, or intrinsically interesting. In the ancestral past, activities leading up to the sating of hunger would have been highly reinforced, and thus food procurement and food processing strategies would have been the primary variables of the reinforcement schedule for individuals with autism. Perhaps, when children with autism ignore their parent's examples of social behavior today, it is because these examples seem uninteresting and meaningless, whereas in the ancestral past they would have been inspired by their parent's hunting and gathering activities. Today, because they are not able to forage or to watch their parents forage and because they can obtain food free of effort, their interests are redirected toward salient, nonsocial activities, like stacking blocks, flipping light switches, lining toys up in rows, playing with running water, chasing vacuum cleaners, and collecting bottle tops. This kind of misapplication of an innate tendency is known in human ethology as a type of "vacuum activity" (Eibl-Eibesfeldt, 2009, p. 153).

The interests of autistic individuals often lead to the development of islets of aptitude or competence. Despite obvious deficits, many exhibit that they have refined or even mastered certain skills. These skills are often referred to as splinter skills. These may include eccentric proficiencies, such as penchants for drawing, music, rote-memory, or puzzle solving (Treffert, 2009). In extreme cases, these skills might include what are often called savant abilities including things like counting, hyperlexia, pattern finding, and calendar or mathematical calculation (Treffert, 2000). Some of these skills and abilities in autism were probably acquired because the individual focused on a particular type of problem solving, they learned to systemize a particular system, and then they retained and

elaborated on the ability. In the past, these elaborate abilities would probably have mapped onto the acquisition of foraging techniques, which, would have been honed to proficiency through rote repetition and practice.

Many anthropologists studying hunter-gatherer groups exclaim that the foragers that they are observing have cultivated amazing naturalistic abilities and are able to sense and perceive things to which they themselves are virtually blind (Kaplan, Hill, Lancaster, and Hurtado, 2000). These abilities, like tracking, ranging, stalking, food processing, mapping of terrain, and knowledge of flora and fauna may be areas through which the potential for autistic or savant-like abilities were channeled in the ancestral past. The same could be said for the deep stores of specialized or technical knowledge exhibited by people on the autism spectrum. This penchant for knowledge about pet interests could have been dedicated to memorizing edible and inedible species, analyzing the habits of prey items, understanding self-protection, maximization of food-collection efficiency, tool fashioning, and shelter procurement.

Aside from their asocial preoccupations, individuals with autism also exhibit stereotyped and repetitive actions (Piven, 2000). In fact, many mammals engage in perseverative or repetitious behaviors especially when placed into unnatural or confining environments (Lewis, Tanimura, Lee, and Bodfish, 2007). Repetitive, stereotypical behavior (including self-injurious behavior) is very rare in the wild but very common in captive animals, as well as in autism (Grandin, 2009). More intelligent animals seem to have increased capacity for self-injurious behaviors. It has been estimated that 10 to 15 percent of rhesus monkeys living alone in a cage develop self-biting, head banging and self-slapping (Lewis et al., 2007). This may indicate that the living conditions that many young individuals with autism experience are artificial, and possibly inhumane, as they are not as stimulating or motivating as the wild environment that they are born expecting.

The propensity toward strict adherence to routine seen in autism may have close analogues in the "master routines" and "subroutines" of many non-social species (e.g., waking, cautious emergence, defecation, grooming, basking, foraging, returning, bedding, sleeping). Although such neurologically mediated rituals can be repetitive and inflexible at times in many vertebrate species, they are important regulators of adaptive behavior (MacLean, 1990). Perhaps the persistent, stereotyped behaviors characteristic of autism had ecological utility in the sense that they allowed structure, order, and self-regulation. Why is there the tendency toward tedium and invariability then? Most of the variety in the life of a human hunter-gatherer is probably found in its social interactions. There would probably be much less variety in the life of a lone hunter-gatherer. A lone forager would be forced to engage in lonely, repetitive, and stereotypic activities, such as scanning repeatedly for threats and items to scavenge, picking and processing fruit, searching for and extracting vegetables, and locating and capturing prey items. An obsessive desire for sameness, repetition, and ritual makes little sense in the context of a social setting but seems applicable in a lone setting. In fact, it might be bad to expect variability and to thrive off unpredictability in a solitary scenario because of the monotony of living alone.

A mind that is highly geared toward using social cognition and forming emotional relationships would have been disadvantageous in an individual who was forced by circumstance to live in a solitary scenario. This may help explain why many individuals

with autism have an undue preference for their own company, pay attention to the non-social aspects of people, and treat others as if they were inanimate objects (Bowler, 2007). Concentrating on empathy or theory of mind would probably have been impractical and counterproductive. Brune and Brune-Cohrs (2006) have speculated that theory of mind and social cognition are probably vulnerable to dysfunction. He pointed out that most people at one time or another have strong desires to ascribe intentions to non-animals. A solitary forager without autism may be likely to attribute agency or ascribe intentions to inanimate objects, amounting to displaced and confused behavior.

In her book "Animals Make Us Human" autistic professor Temple Grandin (who herself engaged in repetitive, restricted and self-injurious behavior at a young age) points out that even though domestic dogs and cats both live comfortably with humans, only cats can leave a human family to live solitarily in the wild (Grandin, 2009). "If you put the family poodle out in the countryside, his chances of surviving are low unless he finds another family to live with. But abandoned cats do fine" (p. 70). Here she underscores the fact that some animals are obligately social whereas others can transition between social and solitary lifestyles. Her life story is an attestation to the fact that individuals with severe autism can make this transition while maintaining the "cognitive coherency" to contribute profoundly to both industry and academia (Grandin, 1996).

Like other animals that are not obligately social, many individuals with autism avoid close bodily contact and fail to establish emotional relationships. It seems that these tendencies might have facilitated solitary life, whereas the inclinations to seek out physical contact and emotional relationships could have made solitary life miserable or unbearable. Classic works of fiction portraying humans abandoned or marooned from others emphasize the human need for companionship. The protagonists in such works frequently have unremitting obsessions with imaginary friends, behavior that would be extraneous and probably maladaptive for a solitary human. People on the autism spectrum would be less likely to yearn for companionship and more likely to focus on survival. Solitary species have very limited abilities for social cognition. This is probably because gregarious predispositions, companionable inclinations, and social instincts in general are maladaptive in a solitary context.

Autistics and orangutans: Solitary foragers

An analysis of the behavior of orangutans in the wild offers valuable insight into the ecology of a solitary ape. Most animals, many mammals, and several species of primates seek out food on their own. It is clear that such a solitary foraging strategy can even be effective for apes. In fact, orangutans, the species that is genetically third closest to humans as revealed by molecular studies, live solitarily in the wild. Orangutans eat, sleep, hunt, and forage on their own (Delgado and Van Schaik, 2000). They are often described as cautious and introverted, and it has been estimated that Bornean orangutans spend at least 95% of their time alone (Van Schaik, 1999). Orangutans have low interaction and association rates, and only infrequently meet up with conspecifics, often only to mate (Van Schaik and Van Hoof, 1996). They have been reported to congregate in small groups temporarily, but only to eat from a particularly fruit-laden tree. Several specialists emphasize that orangutans have limited social aptitude and tend to prefer solitude (Van Schaik, 1999). Van Schaik

(1999) has concluded that, unlike all other species of apes, well-defined communities do not appear to exist in any orangutan population studied so far.

In orangutans, inculcation in infancy and juvenility consists of learning about food procurement from the mother. In stark contrast, chimpanzees are indoctrinated into learning about both food procurement and socialization (Delgado and Van Schaik, 2000). Orangutan mothers teach their babies to recognize edible food species, implement foraging techniques, find shelter from the elements, protect themselves from predators, and develop effective ranging capabilities (Noordwijk and Van Schaik, 2005). Compared to chimpanzees, young orangutans do not learn much from their mothers about communication or socialization; however, they do learn everything that they need to survive and reproduce.

Unlike their orangutan counterparts, chimpanzee adolescents reliably stay with (or at least frequently visit) their mothers for months or years after they have been weaned (Goodall, 1986). Their strong affective ties, emotional attachments, and gregarious nature keep mother and child in contact into adulthood or, at times, throughout life (Galdikas, 1984). Orangutans, on the other hand, exhibit very different behavior. Adolescent orangutans reliably leave their mother and go off on their own to forage very soon after weaning. The bond between the mother and child is based largely on the provision of milk (Noordwijk and Van Schaik, 2005). One of the most frequent complaints of parents with autistic children is that they find it very difficult to build an emotional bond with the child (Frith, 1991). One might imagine that in an ancestral setting the bond between a mother and her autistic child could have been as delicate (and yet at times, as ecologically appropriate) as the bond seen in orangutans. Despite this relative delicacy, the vast majority of babies and children with autism do develop true psychological attachments to their caregivers. This attachment would probably have facilitated the acquisition of foraging techniques as it does in orangutans.

The ability to make inferences about the mental states of others probably first emerged in a clear form during early primate evolution due to heavy selection from the social environment (Brothers, 1990). Apes, relative to monkeys though, have elaborated greatly upon this ability, presumably because their social environment was even more important. Aside from orangutans, all apes, including gibbons, gorillas, chimpanzees, and bonobos are social species, much like humans (Chance and Jolly, 1970). To some degree, it seems that orangutans regressed in their social abilities relative to other apes because, as their group size decreased, pressure from the social environment must have decreased along with it.

Primatologists generally agree that orangutans live solitary lifestyles primarily because the islands of Borneo and Sumatra, where they are found, have poor food density. Relative to the lush African regions that chimpanzees and gorillas inhabit, these islands cannot support large groups of social apes (Delgado and Van Schaik, 2000). If orangutans lived in larger social groups, they would have to travel extremely far (up to 20 miles) each day simply to get enough food to sustain themselves (Sugardijto, te Boekhorst, and van Hoof, 1987). Because orangutans are large animals, and because the trees and bushes in their non-seasonal habitat go through various phases of producing buds, shoots, and fruit, the orangutans must forage through many plants daily to ferret out the right dietary foodstuffs (Delgado and van Schaik, 2000). Because they must traverse so much land

everyday in order to obtain a sufficient number of calories, individual orangutans must define large territories for themselves. It is thought that in Sumatra, each orangutan needs nearly a square kilometer and that in Borneo each requires an even larger area of spatial isolation (MacKinnon, 1974). Fascinatingly, Borneo is thought to be less food-dense, and Bornean orangutans are thought to be less socially inclined when compared to Sumatran orangutans (Van Schaik, 1999). Food density of the habitat is actually known to be an important determinant of group size in a number of animals (Marler, 1968). In fact, when food becomes scarce, even chimpanzees split up to search for food alone (de Waal, 1982).

Harsh and unpredictable climates marked much of the period of human evolution (Reed, 1997). The Pleistocene and Pliocene ice ages caused frequent aridity of the African plains, which would have dried up many sources of food for our foraging ancestors (Ravelo, Andreasen, Lyle, Lyle, and Wara, 2004). These conditions would have rendered our habitat nutritionally scarce (Bobe, Behrensmeyer, and Chapman, 2002), perhaps forcing groups of our ancestors to disband. Humans may have been forced to do this habitually in the past despite the fact that we are an inherently social species. In sum, environmental forces prominent during our evolution caused nutritional scarcity that, at least in some geographic regions, may have created the same conditions that selected orangutans to become solitary. Another condition that influences selection for sociality is the distribution of food resources. It is known that when food is approximately evenly dispersed in an environment, solitary foraging yields higher energy returns, but when food is clumped, group foraging becomes more efficient (Marler, 1968). One may not even need to invoke scarcity or food distribution patterns to conclude that many pre-social species, including humans, may have experienced historical disruptions (either punctuated or gradualistic) in their social continuity that left lasting traces in the genome.

Adaptations particular to orangutans, which are thought to reflect their life-history strategies, may have implications for autism. Orangutans exhibit prominent sexual dimorphism (van Schaik, 2004), and much of this is thought to be due to high testosterone levels in the males. Autistics are also thought to exhibit elevated testosterone levels, which may be associated with increased fetal exposure to testosterone (Knickmeyer, Baron-Cohen, Raggatt, and Taylor, 2005). It might make sense that a solitary strategy is better suited to males given that female animals of many species have an increased need for social support and parenting proficiency. Male orangutans actually spend a greater proportion of their time alone compared to females (most of the time spent between two males is thought to be attributable to random, unintended encounters) (van Schaik, 1999). Interestingly, autism is four times more prevalent in men compared to women, is accompanied by more severe anomalies in brain structure in men, and is known to have a worse prognosis in men (Bowler, 2007). Higher testosterone levels in autistic males may have increased their sexual aggressiveness as well as their sexual attractiveness. Mating practices of individuals on the autism spectrum may have been similar to those of the orangutan. Females with autism or on the autistic spectrum probably had little difficulty in procuring receptive sex partners. Males, on the other hand, could have procured partners using the same tactics used by male orangutans, such as propositioning, perseverative soliciting, provisioning, food sharing, and others.

It has not yet been made clear how much orangutan neurology has been affected by

their recent stint of solitary foraging, which may have only gone on for the last 10,000 years (Van Schaik, 1999). Regardless, evolutionary comparisons with solitary primates and other solitary mammals that are known to have neurological adaptations causing them to lack biological instincts for gregariousness, affection, and strong social relationships should be informative. It is also important to affirm that no offense is intended toward autistic individuals in this comparison with orangutans. Only traits related to sociality are compared here, and individuals with autism are not in any way equated with apes in general. In fact, individuals with autism are only compared to orangutans here to the same extent that neurotypical individuals are compared to chimpanzees. Orangutans were selected as a basis of comparison for this article simply because they are the species of solitary foragers that is most closely related to humans.

The evolution of autism

The evolution of social tendencies in animals is a poorly understood topic of research. Even less understood is the evolution of solitary tendencies from social forebears. It is clear that there are costs and benefits to living in groups and that the pressures from the social environment can change abruptly (Perez-Barberia, Shultz, and Dunbar, 2007). Surely, in the past, individuals on the autism spectrum were sometimes born into the arms of supportive and cohesive social groups, much like today. If autism does represent a solitary forager strategy, then this circumstance could have constituted a mismatch that may have been negatively selected against. However, most adaptations have risks associated with them and instead of representing a panacea; they reflect tradeoffs that, over evolutionary time, produce on average more benefits than costs. This mismatch may not even have decreased fitness. Given the propensities of modern day people with autism, such individuals might have chosen to journey off alone nomadically or hermitically. Alternatively, they might have chosen to forage alone but return to their group infrequently in order to interact and travel with group members. This may have depended on "how autistic" the individual was. Even individuals on the far side of the autism spectrum may not have even been truly solitary during prehistory. Social chess abilities or Machiavellian intelligence are not well developed in people on the autism spectrum. Their speech and mannerisms can be monotonous and mechanical, yet this may not have kept them from offering valuable skills and forming functional relationships with other humans. In many cases, autistic individuals exhibit pragmatic competence that could have made them valuable attributes to their foraging companions. Today, a large proportion of individuals with Asperger's have been assimilated into elite social and professional spheres despite the fact that they are not adroit social conformers (Grandin, Duffy, and Attwood, 2008). It is reasonable to imagine that a proficient hunter with autism could be not only tolerated but highly valued by a small band of hunters who were each eccentric themselves, not having been exposed to our modern, relatively conformist, post-industrial society. This would be akin to the situation today where millions of mainstreamed autistic children around the world have become accepted on the playground, despite their differences. It is well accepted that despite valuing their time alone, many individuals with autism enjoy friendships and have a documented predilection for valuing quality of friends over quantity (Bauminger et al., 2008). Similarly, when in captivity, or when gathering around a large,

fertile fruit tree, orangutans can be observed to have social competencies, even if they are not as facile or effusive as chimpanzees.

If autism in fact evolved, did it do so predominantly among neurotypical humans or within an isolated population of solitary individuals? The autism continuum could represent a remnant of genetic introgression that took place before humans were the lone species in our genus. Perhaps some of the genes for autism evolved not in our direct ancestral line but in a solitary subspecies which later merged genetically with our line of descent through gene flow. Demes, or subpopulations of relatively solitary individuals, could have been assimilated into our gene pool after a fair amount of interbreeding following migration. Such solitary subpopulations could have arisen in ecologically or climatologically different geographic regions of Africa anytime during the Plio-Pliestocene.

The evolution of human populations with short stature may shed light on this issue. The pygmy phenotype, characterized by small body size, appears to have evolved independently in South American, African, and Southeast Asian populations in the last 200,000 years. The phenotype is mostly restricted to rainforest environments and is thought to represent a response to the selective pressures associated with living in a tropical rainforest (Migliano, Vinicius, and Lahr, 2007). This powerful climatological association has motivated adaptationist hypotheses as to how small size would increase reproductive success in a warm, wet environment with dense foliage. Physical anthropologists have hypothesized that short stature may have increased the capacity to cope with one or more of the following: caloric limitations, high temperature, high humidity, extensive forest undergrowth, increased mortality, vitamin deficiencies or even a combination of these (Migliano et al., 2007). Multiple genetic disruptions of the growth hormone and insulin-like growth factor I pathway are likely to be involved etiologically, but no specific DNA mutations have been uncovered (Cavalli-Sforza, 1986). It is clear though that when pygmies intermarry with non-pygmies, the result is a spectrum; children tend to be intermediate in stature to those of the two parental populations (Cavalli-Sforza, 1986). Pygmy populations show us a few things that are interesting in the present context: 1. isolated pockets of humans can remain reproductively insulated for long enough to evolve discrepant ecological strategies; 2. such populations can quickly (less than 40,000 years in the South American and Asian pygmies; Cavalli-Sforza, 1986) develop features that vary markedly from the norm; 3. these traits can involve multiple genes at different loci; and 4. interbreeding can result in either continuous or polymorphic variation in subsequent generations. It is interesting to note that, as these indigenous people become assimilated into other gene pools, the genes for short stature will persist and may affect phenotypic variability in sporadic and unpredictable ways for a long time to come.

The genes that make up a polygenic trait usually all have different natural histories. They appeared as mutations at different periods, and they were selected at different times. For example, several different genes, each working through different molecular mechanisms, helped Europeans develop lighter skin as they moved to higher latitudes over the last 60,000 years. Interestingly, an entirely different set of alleles with unique cellular properties helped people in northern Asia develop lighter skin (Norton et al., 2007). Few of these genes have been selected to fixation, and they occur together in different proportions, creating a lot of variability in skin color even within isolated populations. The genes for

autism may be similar to these examples in the sense that each gene may have a different natural history. Some genes may have been meant to work cooperatively whereas other have not. Each gene that predisposes toward autism may represent a different way to make an organism a little less reliant on sociality.

Like other polygenic, continuous traits, the mutations responsible for autism could have been maintained by "environmental heterogeneity," a form of balancing selection. In other words, the genes responsible for autism may have remained in our gene pool because as social-environmental conditions fluctuated in the past, discrepant genetic polymorphisms, or "multiple alternate alleles," were favored. Currently, it is not possible to scrutinize the natural history of autism genes at this level of analysis because, even though over a dozen genes have been implicated, including an oxytocin receptor, a serotonin transporter, and putative language genes, very little agreement exists in the literature over the specifics (Cantor, 2009).

It is currently not possible to tell whether the frequencies of genetic variants responsible for autism are high enough, or in the right proportions, to accommodate a model of past positive selection. The contributions of a large number of relatively rare genes and of de novo mutations (Abrahams and Geschwind, 2008) tell us that autism may not have been subject to natural selection for thousands of years and that it may have a large non-evolutionary component, as well as an irregular evolutionary signature. The present article cannot fully address this issue primarily because of the lack of knowledge about the genetics of autism. It is unclear whether autism can be explained better by rare mutations or by rare combinations of common genetic variants (Muhle, Trentacoste, and Rapin, 2004). Future linkage and association studies though may be able to resolve whether the responsible genes are mutated sequences encoding aberrant gene products or normal polymorphisms acting synergistically (Kumar and Christian, 2009). It is also clear that a certain proportion of the clinical picture of autism is not representative of adaptation. Some cases of autism are associated with congenital anomalies and physical stigmata that were probably not adaptive. How and why rare comorbidities such as Rett syndrome, tuberous sclerosis, fragile X syndrome, psychomotor epilepsy, and other clinical entities can present with autism is far from apparent (Amaral et al., 2008). It may be the case that several pathological conditions present symptoms that resemble autism (or exacerbate autism) and thus clinicians and epidemiologists have grouped them together with autism, obscuring its natural visage and the elements of it that could have been adaptive. This is certainly the case with ADHD and schizophrenia. Idiopathic or teratogenic neurodevelopmental insults can closely mimic these as well as other neurodevelopmental disorders (Zimmerman, 2008). Many of these unknowns will not become clear until additional genetic, molecular, and pathophysiological research is done.

Another important criticism of the present argument is that there may be no clearly documented anthropological evidence for solitary foraging in modern humans. This shouldn't be taken as significant evidence against the present hypothesis given that there do not seem to be any documented examples of autistic individuals in hunter-gatherer groups either. It seems that no one has looked for these things systematically. The prevalence of autism in forager groups should be equivalent to the prevalence in the rest of the world, given that epidemiologic studies indicate that environmental factors, such as perinatal

insults, prenatal infections, teratogens, and toxins (factors that may be particular to modern life) account for only very few cases of autism (Amaral et al., 2008). In modern society, it is apparent many people intentionally sequester themselves or prefer solitude to different degrees, and it is reasonable to expect that this type of behavior would have existed in the ancestral past and could have been continuous with the autism spectrum. Despite the fact that there seems to be no academic literature on solitary foraging in humans it is clear that when food is scarce, hunting parties have been seen to disperse for solitary hunting and reconvene at later times (Hill and Kaplan, 1993; Jochim, 1988). When food is not abundant and nutritional intake is low, the optimal foraging strategy is to lower population size and density (Belovsky, 1988). As with other apes, submarginal or impoverished habitats cannot support large groups of humans, and group size diminishes under these circumstances (Mandryk, 1993).

Several substantiated cases of abandoned youths, known as feral children, have survived to adulthood in the wild (Brothers, 1990). It is probable that a much larger proportion of children were orphaned in the wilderness in ancestral times, and this may have contributed to the selective pressures for asocial temperament. Feral children usually have many autistic features in the sense that they are emotionally detached, prefer solitude, and eschew physical contact (Brothers, 1990). These features may constitute protective, adaptive responses to solitary life, and their resemblance to the symptoms of autism may not be coincidental.

A consistent, predictable proportion of ancestral humans (and ancestral hominins) must have been forced to live alone during the six million years of human prehistory. From these individuals, the ones with mutations that created disruptive abnormalities in regions of the social brain may have experienced increased reproductive success. This should not sound like a stretch, considering that this general pattern may have already occurred during the evolution of orangutans. After orangutans diverged from the common ancestor that they shared with gibbons around 18 million years ago, they moved into Southeast Asian rainforests where they were forced to give up their social lives for solitary ones because of ecological constraints (Sugardjito et al., 1987). It appears that from the consistency of their behavior in and out of the wild, their solitary tendencies may be hereditary and neurological. For this reason, it should be very informative for autism researchers to compare the brain areas responsible for social cognition across apes. This kind of research has not yet been done. We may never know exactly what it was like to have autism in prehistoric times, but comparing them to known solitary species on a variety of neurological measures may provide clarification.

The brain in autism

The brain abnormalities in autism do not seem to constitute indiscriminate pathological abnormalities as one might expect if autism were simply a disease. The most conspicuous brain abnormalities seem to consistently and systematically affect the areas of the brain that have been associated with social cognition (Adolfs, 2001). The amygdala, the anterior cingulate cortex, the orbito and medial frontal cortex, and the mirror neuron system have all been strongly associated with social cognition (Dapretto, Davies, and Pfeifer, 2006), and also have been shown to be the same areas that exhibit the prominent anomalies

in autism (Williams, Whiten, Suddendorf, and Perrett, 2001). This selectivity makes it seem that the genes that influence social areas of the brain were affected and the others were spared (consonant with Baron-Cohen's psychological theories of autism). According to Gelman and Williams (1998), brains have been evolutionarily organized to acquire and store particular sorts of relevant information and disregard other, irrelevant information. In this context, individuals along the autistic spectrum appear to have a neurological propensity to gate out social information and thus gain conscious access to highly processed nonsocial perceptions and schemata. This section will look at how this might be accomplished by focusing on eye contact, facial expression, oxytocin regulation, macrocephaly, amygdala reactivity, and facial recognition in autism.

Curious phenomena that are very common in autism are averted gaze and poor eye contact (Hutt and Ounsted, 1966). Autistic individuals describe eye contact as uncomfortable and even threatening (Piven, 2000). Interestingly, eye contact is also very rare in the vast majority of solitary species, including orangutans, who actively avoid both direct gazing and even facing (Yamagiwa, 1992). Chimpanzees and gorillas share gazes and use the eyes for communication frequently, just like most humans (Gomez, 1996). Chimps and gorillas use eye contact constantly while interacting with members of their own group but may charge at an individual from another group if it makes eye contact. Staring between unfamiliar apes is often interpreted as a threat signal; therefore, it is best for a solitary mammal to avoid both eye contact and direct gazing in order to forestall an attack (Gomez, 1996). Orangutans actively avoid gazing and eye contact and this tendency, very common among solitary animals, has been explicitly interpreted as adaptive for their solitary foraging niche (Yamagiwa, 1992). Instead of face-to-face direct viewing, orangutans, like individuals with autism, glance momentarily at others sideways with the head turned away (Kaplan and Rogers, 1996). The neurological substrates (including amygdalar sensitivity) that underlie this very specific and prominent tendency may have evolved for the same adaptive, defensive reasons in both autistic individuals and orangutans.

Studies have shown that autistic individuals are less expressive, especially with respect to facial communication. They make fewer facial expressions and are rated as more flat or neutral in affect by observers (Yirmija, Kasari, Sigman, and Mundy, 1989). This absence of facial responsiveness is probably due to underlying neuronal mechanisms, and there is evidence that the facial motor nucleus is significantly reduced in size in autism (Rodier, Ingram, Tisdale, Nelson, and Romano, 1996). Fascinatingly, the size of the facial motor nucleus is thought to vary predictably in total volume as a function of group size in monkeys and apes. The larger the average group size, the more important facial expressiveness is and the larger the facial motor nucleus must be (Sherwood, 2005). It should be informative to analyze the anatomical organization of the autistic facial motor nucleus, taking note of the general size, the placement of motor neurons, distribution of neuron types and the general topography of muscle representation. Experts in phylogenetic specializations of primate facial neurology might be able to perceive social or ecological traits in the distinctive anatomical organization of the facial neural pathways in autism. Analyzing it relative to that in orangutans should be informative as well, as it is known that orangutans are much less facially expressive than other apes (Liebal, Pika, and Tomasello,

2006).

Oxytocin, a neuropeptide thought to enhance social learning, social expressiveness, direct eye gaze and the ability to remember faces (Savaskan, Ehrhardt, Schulz, Walter, and Schachniger, 2008), is reduced in autism subjects. Diminished peripheral levels of oxytocin may play a large role in retuning social brain modules in autism (Green et al., 2001). It has been shown that intravenous oxytocin produces a significant reduction in stereotypic behaviors in adult autism subjects and increases empathy in people without autism (Hollander et al., 2003). Variation in oxytocin levels in mammals reflects adaptations to the social environment, just as it may in the case of autism. Animals that rely on pair-bonds and social attachment have higher levels of plasma oxytocin, especially when it is behaviorally relevant, like during childbirth or monogamous sex (Campbell, 2008). Comparing prairie voles to montane voles, two very closely related species of rodent, is interesting in this context because the two differ widely in bonding behavior. The montane vole, relative to the prairie vole, has a much smaller number of receptors in the brain for oxytocin and, unlike the amorous prairie voles, they do not form pair bonds (Marler, 1968). The montane voles have fewer receptors and thus are less responsive to oxytocin, making them more wary, suspicious and more easily frightened of other members of their species—ensuring that they do not allow themselves to become vulnerable (Marler, 1968). It is thought that the wide discrepancy in social behavior between these two species reflects adaptation to two very different physical and social environments (Adolfs, 2001). Not surprisingly, interspecific, seasonal and reproductive variation in oxytocin concentrations have been attributed ecological and adaptive significance. High levels are associated with trust, love, pair-bonding and generosity in a variety of mammals (Adolfs, 2001). It would be interesting to compare the details of oxytocin action—such as receptor number and distribution—in solitary animals with that of people with autism.

Diminished peripheral levels of oxytocin may cause individuals with autism to be born "expecting" or prepared for a socially impoverished environment. Natural selection cannot act on behavior directly but instead acts on the neural substrates that generate the psychological mechanisms that create the behavior. Evolved psychological mechanisms, such as cognitive modules, are generally understood in terms of specific inputs, decision rules and outputs (Buss, 1995). Most of these mechanisms were naturally selected to be sensitive to a narrow range of perceptual information. In other words, they are biologically prepared to learn about or solve particular adaptive problems. Some mechanisms are known to be domain-specific and many of these are assumed to exhibit variation in humans, causing some people to attend to perceptual cues that others might miss entirely. Tuning differences in domain-specific mechanisms or modules, especially those involving oxytocin, serotonin and adrenaline, may underlie the differences in autistic cognition and, like other differences seen in nature, may have been created by natural selection to help solitary foragers face their particular set of recurrent or ecologically relevant threats and opportunities.

It has been shown that one or both hippocampi are often significantly larger in autism (Amaral et al., 2008). The hippocampus is a convergence zone that is integral to spatial ability, and perhaps the large size of the hippocampus in autism has neuroecological relevance. The study of neuroecology focuses heavily on the relationships between

ecological hardships, necessity for spatial ability and the size of the hippocampus (Garamszegi and Eens, 2004). It might make sense that a solitary forager would have to compensate for the fact that it could not rely on the spatial abilities of its companions. Individuals with autism have also been shown to excel at the block design subtest of the Wechsler intelligence scales, evidence of high visuospatial abilities (Bolte, Dziobek, and Poustka, 2009). It may be possible that such abilities are indicative of the visuospatial or mnemonic rigors particular to a solitary existence.

Brain growth is accelerated in early autism, and this may have been adaptive for a youngster that was preparing to become a solitary forager. Individuals with autism have been known for years to exhibit increased head circumference and increased brain size (two highly correlated traits) during infancy (Dementieva et al., 2005). Macrocephaly (head circumference higher than the 97th percentile), one of the most consistently encountered traits seen in autism, is known to affect between 14% and 34% of all autistic infants (Fidler, Bailey, and Smalley, 2000). In fact, total brain size, as revealed by MRI, is on average 5-10% bigger in autism between 18 and 48 months of age (Mraz, Green, Dumont-Mathieu, Makin, and Fein,, 2007). Neonates who will develop autism and macrocephaly exhibit normal head circumference at birth, but their head growth accelerates during the first year of life. This growth continues until at least 4 years of age, slows and then decelerates prematurely (Dementieva et al., 2005). This increased rate of brain maturation and growth slows early, well before nonautistic brains start to slow, resulting in very similar head sizes between those with autism and those without in both adolescence and adulthood (Fidler etal., 2000). A large contributor to increased brain size in youth is myelination, and it is thought that different areas of the brain myelinate differentially according to an ecological program where primary sensory areas begin to myelinate first, well before association cortices. The dramatic increase in head circumference from birth until age 4 may be evidence that the learning arc for a solitary forager is not as protracted as it is for other children. Hunter-gatherer children need to laboriously and perseveringly learn a language along with social morays, a time-consuming process (Kaplan et al., 2000). Researchers have concluded that learning during human childhood takes so long because social interactions are more variable and relatively less frequent than other forms of ecological learning (Greenough, Black, and Wallace, 1987). The fact that individuals with autism show this increase in head and brain size between birth and age 4 may indicate that they are programmed to learn more about their environment, faster, at an earlier age. This may also suggest that autism represents a precocial ("out of the nest early") strategy where learning takes place very early so that the animal can become independent of its mother quickly, a characteristic observed in countless nidifugous animals that do not have complex social lives. Consistent with this conclusion are data evincing that many males with autism exhibit precocious puberty (Tordjman, 1997), further evidence of a precocial as opposed to an altricial strategy.

Other neurological differences particular to autism may hold neuroecological significance. Individuals with autism have been widely reported to have increased fear activity in the amygdala and high levels of anxiety (Baron-Cohen et al., 2000) which might act to increase vigilance, caution and a healthy fear of strangers. It seems reasonable to assume that a solitary forager would benefit more from such caution than would an

individual who must learn to embrace companions. Some frequently reported, but only preliminarily researched, eccentricities in autism include acute and perceptive hearing, and increased frequency of, and interest in, smelling (Leekam, Nieto, Libby, Wing, and Gould, 2007); two features that could certainly be interpreted in a neuroethological context. Face processing, a key factor in the development of social perception, is severely impaired in autism (Dalton et al., 2005). The area responsible for face recognition, the fusiform face area, in particular has demonstrated reduced activation in autism during facial discrimination tasks (Pierce and Redcay, 2008) indicating that in autism, like in many solitary animal species, identity recognition may not be as valuable. These neurological differences may be telling. If autism truly does represent a solitary phenotype, then the brain abnormalities—which are highly consistent across individuals on the spectrum—should furnish theoretically intriguing insights, not only into comparative cognition but also into human evolution.

Implications of the Hypothesis

This article has attempted, in an exploratory manner, to provide a characterization of autism that reconciles known findings with evolutionary theory. In the past it was not understood how individuals on the autism spectrum might have gotten along during prehistoric times. Yet now, a comparison with solitary species shows that autistic individuals may have lived largely solitary lives and achieved self-sufficiency and reproductive success. Characteristics of autism that have been interpreted as consistent with the solitary forager hypothesis include: the high systemizing abilities, the obsessive and perseverative tendencies, the repetitious and ritualistic tendencies, splinter skills, the deep but narrow stores of knowledge, the parallels with orangutans and montane voles, gaze aversion, absence of eye contact, increased hippocampal size, macrocephaly, precocious puberty, the testosterone effect, reduced fusiform face area and facial motor nucleus activity, amygdalar sensitivity, reduced oxytocin concentrations and the sex ratio. Clearly, there are exceptions to each of the lines of evidence offered here. For instance, there are innumerable functional differences between the social mind of an orangutan and that of the average individual with autism. The growing body of experimental literature testing the social-cognitive skills of solitary species may offer important insight into autistic traits though and tell us more about the similarities and differences in these domains. It will be very difficult to determine irrefutably if what we know as autism today was in fact an adaptive phenotype in the ancestral past. The hypothesis presented here is underspecified and vague but may be progressive as it is thought that analyzing disease states from an evolutionary perspective can ultimately do much to inform and influence medical theory and, ultimately, even intervention strategy (Nesse and Williams, 1995). Furthermore, the evolutionary perspectives delineated here could potentially provide structure for empirical investigations in animal behavior or cognitive neuroscience.

The case that the autism spectrum represents a solitary forager phenotype is a very top-heavy argument that can and probably should be toned down in numerous ways. First, individuals with autism were probably not totally solitary and may even have been better adapted to very small groups than to a purely solitary existence. Second, it should be

emphasized that natural selection may have only been selecting for subclinical autistic traits and that the high-functioning corner of the spectrum may have been the substrate for natural selection. Third, the most severe cases of autism may actually have been maladaptive and due to assortative mating of two individuals that hold a high number of autism susceptibility genes. A comprehensive solitary forager theory of autism must address these issues and should start by partitioning variation in autism into nosological categories that represent either pathology or nature. This article has not clearly committed to delineating which aspects of autism are adaptive and which are not, or even committed to whether the lowest functioning forms could have had a place in nature. It is probably too early to make these discriminations. However, it seems that if the extreme end of the autism spectrum was selected for, that the distribution of autism prevalence relative to severity might be bimodal or have a fattened tail, yet this does not seem to be the case.

It is probable that other endophenotypes and genetic patterns in autism can be analyzed in terms of the present hypothesis to provide convergent evidence. Eventually, genetic hypothesis testing could provide near incontrovertible proof for the present hypothesis. Until then, comparing intron relative to exon mutations in susceptibility genes for autism, mapping gene linkages, analyzing epigenetic patterns, scrutinizing genome-wide microarray analyses, and even looking for inter and intraspecific trends in genographic data may all provide support. Further comparative behavioral studies may also be revealing. It will be instructive to look for abilities in autism that more closely resemble foraging activities than the abilities mentioned here. Conversely, looking for anthropological evidence for autism-like traits among successful foragers should also be revealing. It is also important to question whether the processing deficits or cognitive findings in autism might have put a solitary forager at a disadvantage. In order to further explicate the evolutionary roots of autism and draw new inferences with the potential to inform medical intervention, I encourage researchers to turn to ethology and Niko Tinbergen's (1963) "four questions" in understanding the value of behavior: 1) what is the immediate benefit to the organism? 2) What is the immediate consequence? 3) How does it develop in the individual across ontogeny? 4) How did it evolve in species across phylogeny? Knowledge about the costs and benefits of solitary existence may help to guide each of these lines of research.

Oliver Sacks (1970) has formulated an interesting view of autism that appears to be consistent with this. He points out that the perspective of the autistic individual appears aboriginal because they never succumb to our modern societal conventions, but that this does not keep them from perceiving, thinking and behaving in original, innovative and intelligent ways:

> The autistic by their nature are seldom open to influence. It is their "fate" to be isolated and thus original. Their "vision," if it can be glimpsed, comes from within and appears aboriginal. They seem to me, as I see more of them, to be a strange species in our midst, odd, original, wholly inwardly directed, unlike others. (p. 230)

Studies in behavioral genetics have demonstrated that tendencies for cooperation,

temperament, and sociality have biological underpinnings. Furthermore, they show considerable variability within and between animal species (Frank, 1998). Tendencies for independence, reclusiveness, introversion and other traits characteristic of autism certainly show a great deal of variability between species (Trivers, 1985), but what about within them? Perhaps populations of other social species, such as chimpanzees, have an equally low but consistent prevalence of autistic individuals as well. No formal diagnostic criteria are available for psychiatric or even social disabilities in other animals (Wilner, 1991), but it would be interesting, although difficult, to see if there are analogues, or possibly homologues of autism in other species. If there were homologues of autism in species closely related to humans, it would be relatively easy to use molecular techniques to show this given that the genes responsible could be identified. Looking at the evolutionary signatures in the behavioral genetics of autism might tell us more about the variability in life-history strategies of our ancestors. Many different factors could be invoked in such a discussion, including behavioral neuroscience, cognitive primatology, the importance of group membership to survival, fission-fusion sociality, mating strategies, maverick males, paleoneurology, parenting methods, phenotypic plasticity, sexual selection, social and affective neuroscience, pair bonds, territoriality, social hierarchy, and others.

> Because humans are highly social, we like to think that complex societies represent the crowning achievement of evolution.… Indeed, if group living were the universally superior lifestyle, we would expect social species to outnumber solitary ones, but exactly the opposite is true. Why? Almost certainly because in many environments, the costs of living with others are prohibitively high. (Alcock, 2001, p. 118)

Humans are an innately social and gregarious species. Their ancestral environment, like that of chimpanzees, selected them to be this way (Foley and Gamble, 2009). It is probable that as with all traits selected for by evolution, there are costs and benefits associated with social predispositions and that the large variation in sociability in our species reflects the large variability in selective forces in the past. The relative prevalence of autism is high enough to suggest that it was a phenotype that was naturally selected for in the past, but also low enough to suggest that it was rarely preferable to the socially typical alternative. Perhaps the prevalence of the autism spectrum in modern human populations tells us something profound about the frequency of forced solitude in ancestral times, the adaptive value of social instincts and the plasticity of human cognitive strategies. Showing that autism had ecological viability and that it exists today because of its success in the past suggests that it should not be considered a disease, but instead a condition. It should not be thought of as something to be ashamed of, but as something that represents individuality, self-determination and autonomy.

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